

GONYAULAX POLYGRAMMA STEIN IN CAPE WATERS: A TAXONOMIC PROBLEM RELATED TO DEVELOPMENTAL MORPHOLOGY

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ABSTRACT

During an occurrence of "Red Tide" in False Bay, a large number of individuals of *Gonyaulax polygramma* Stein were examined. They showed a range of variation related to the inferred development morphology of the thecae. This range encompassed the characteristics of many of the species within the "*Polygramma* group". A description and figures of the local population are given, and also observations on the alternation of thecate and encysted stages. The characters of the species within the "*Polygramma* group" are tabulated, and attention is drawn to an apparent developmental series within it which tends to show an affinity between some, if not all, of the species closer than at specific level.

A species of *Gonyaulax* was the causative organism of a "Red Tide" associated with marine fauna mortality in False Bay during March, 1962. Many individuals were examined throughout this period. Exact identification was problematical due to the range of morphology displayed. In general it conformed to the description of *G. polygramma* Stein as elaborated by Kofoed (1911), Lebour (1925) and Schiller (1937), although it was consistently smaller than the figures given. Comparison with other species in the "*Polygramma* group" in Kofoed (1911), and Kofoed and Michener (1911) led to confusion, as the characters by which they are distinguished are variably shown by many individuals of the local population. However, from the wealth of material available it was highly probable that a developmental series within only one species was present.

The following is a diagnosis of the population investigated:

Body subspherical to slightly elongated, varying between 1.1 and 1.3 transdiameters in length. Epitheca broadly angled at the apical-precingular suture, a small truncated apical horn being apparent in some individuals. Hypotheca hemispherical, sometimes fuller on the left side. Girdle descending, variably displaced from 1 to 1.5 girdle widths; deeply impressed, with spiny lists present on older thecae. Ventral area indents the epitheca to a greater or lesser extent; the width between the girdle ends being variable, and a flexure to the right generally exhibited on the epitheca. Posterior ventral plate subcircular, indenting the antapical plate.

Plate formula: 3', 0^a, 6'', 6, 6''', 1^p, 1'''. Ventral pore on apical 3'. Precingular 6'' quadrangular, sometimes almost square. Postcingular 1''' small and elongate, varying between 0.4 and 0.8 girdle-widths across. Posterior intercalary large and elongate. No clear subdivisions of the intermediate plate visible.

Surface markings primarily longitudinal, anastomosing of side branches leading to a reticulate appearance on older thecae. No pores visible on the surface except for the ventral pore. Spines occur on the surface, particularly on the hypotheca, becoming pronounced on the older thecae.

Dimensions: Length 29–48 μ

Transdiameter 22–34 μ

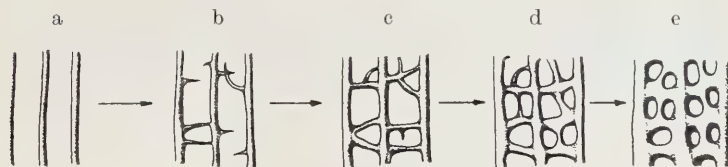
Girdle width 4–5 μ

The longitudinal flagellum extends for twice the length of the cell.

From the material at hand the following stages of the life cycle are inferred:

Ecdysis occurs by a rupture of the apical and precingular plates to release the cell-contents which protrude from the apical pole in much the same way as that figured by Schiller (1937, fig. 301, g.). The released cyst is of a characteristic shape, rounded, and with a protuberance marking the apical pole. The cyst has a predominantly golden-brown colour due to the large number of chromatophores, in this case peripherally arranged, the nucleus appearing as a dark-green, granular area. No dividing individuals were seen, although the cysts often occurred in dense clumps which could have been a result of division. Kofoid and Swezy (1921) have indicated that in autotrophic marine forms encystment commonly provides protection during the non-motile stage accompanying binary or multiple fission. It is likely that it was during encystment that the local autotrophic population underwent fission.

Each cyst forms a new theca, and the impression of the girdle and sulcus becomes apparent (pl. 1, fig. 5). The newly-formed thecae show the plate pattern clearly (pl. 1, figs. 1, 2). Faint lines develop longitudinally, and at this stage no spines, antapical or otherwise, are visible. The body form is rotund. In the intermediate thecate stage (pl. 1, fig. 4) the lines become more marked, and lateral outgrowths connect them to form a reticulum. Linear markings also appear on the girdle plates. Antapical spines develop, the greatest development being apparent in connection with the left antapical spine which becomes markedly longer (up to 7 μ) in most individuals, but not all. The older thecae (pl. 1, fig. 3) show considerable development of the surface reticulation, until in some cases the linear nature can become masked by a thickening of the anastomoses. The girdle markings become reticulate by subsidiary outgrowths, ultimately leading to a porulate appearance.



TEXT FIG. I

Surface marking series.

- a. linear early stage.
- b, c. linear-reticulate intermediate stages.
- d. reticulate on old thecae.
- e. porulate (observed on girdle only).

The marked surface spines of the older thecae appear to be a character limited to the local population. They are most developed on the hypotheca, and around the girdle margin. In some individuals they mask the antapical spines. A small web was sometimes visible associated with the left antapical spine.

The older thecae were more elongate than the younger ones. A strong greenish-white luminescence was apparent when a living sample was agitated, and this was noticeable in the sea when the "Red Tide" occurred.

G. polygramma Stein is chiefly distributed throughout tropical and subtropical waters. Kofoid (1911) refers to its association with "Red Tide", but it has never been recorded as a causative organism of the phenomenon, and never associated with marine fauna mortality.* Karsten (1907) records it from the Indian Ocean, but it is not listed by Hart and Currie (1960) as present in the Benguella Current. The author found it present in small numbers in the cold waters west of Cape Point, and proliferating in the warmer False Bay waters.

It is pertinent at this stage to consider the species within the "*Polygramma* group". Kofoid (1911), in his monograph on the genus *Gonyaulax* described five species, three being added by Kofoid and Michener (1911). They all possess the same plate formula, and are characterised by predominantly linear longitudinal markings. The eight species can be arranged in a series of increasing size which is combined with an elongation of form, increasing antapical symmetry and an increasing density of surface markings. Kofoid noted this series, but did not draw attention to the increasing density of surface markings as it is possible that he considered the porulate condition of *G. kofoidi* Pavillard and *G. pacifica* Kofoid as a simpler state than the more reticulate species. However,

* Since the paper was submitted one reference to its being highly destructive to oyster beds in Japan has been found. Anon. (1933), *Nat.* 132 : 253.

from the present author's observations on the development of surface markings, particularly on the girdle which culminate in a porulate appearance (Text fig. 1), it would seem possible to infer that the porulate condition constitutes an end-point in an increase of surface reticulation without the formation of spines.

TABLE I

Characters of the species within the "Polygramma" series.
(Figures compiled from the referred literature.)

(t) = quoted in text of Kofoid (1911)

(d) = quoted in diagnoses in Kofoid (1911)

Species	Length μ (L)	Trans- diam. μ (TD)	$\frac{L}{TD}$	Markings
<i>G. minuta</i> Kof. and Mich.	20-25	18-20	1.1	linear
<i>G. turbynei</i> Mur. and Whit.	32-47	26-37	1.16	lin.-reticulate
<i>G. scrippsae</i> Kofoid	29-50	27-40	1.12-1.15	lin.-reticulate
<i>G. pavillardi</i> Kof. and Mich.	48	44	1.1	lin.-reticulate
<i>G. polygramma</i> Stein	42-75	38-48	1.2-1.5	lin.-reticulate
<i>G. reticulata</i> Kof. and Mich.	50-65	45-50	1.3	reticulate
<i>G. kofoidi</i> Pavillard	77-110 (t)		1.5-2.0 (t)	
	100-110 (d)	62-65	1.65 (d)	poroid
<i>G. pacifica</i> Kofoid	106-179 (t)		1.5-1.75 (t)	poroid
	148-167 (d)	72-88	1.6-2.0 (d)	

According to Kofoid the species within the group can be separated from each other on the combined grounds of dimensions, displacement of the girdle, the shape of certain plates, the presence or absence of antapical spines, and the pattern and degree of surface markings. In view of the continuum in size and development of surface markings as shown by the arrangement in Table I the presence of a single-species complex is strongly suggested. This view is strengthened by the present author's observations which show great variability among the other factors in the local population considered referable to a single species.

Kofoid (1911, p. 231) admits infraspecific variability in *G. polygramma*, drawing attention to the existence of variants within the species grading towards adjacent members of the series: "This widely distributed species varies toward both *G. turbynei*, the next smallest member of the series, and towards *G. kofoidi* and *G. pacifica*, the longer ones". He maintains that *G. turbynei* can be distinguished from *G. polygramma* by its lack of antapical spines and lack of an apical horn. However, both these factors were variable in the population investigated. He separates *G. polygramma*, *G. kofoidi*, and *G. pacifica* by a comparison of size, shape of the antapex,

and width of the posterior intercalary plate, all factors manifesting the graded change shown by the arrangement of the series. Schiller (1937) suggested the possibility of *G. kofoidi* and *G. pacifica* being the same species.

There would appear to be a close affinity between those species discussed above, and this affinity would appear to embrace *G. minuta*, *G. pavillardi*, and *G. reticulata* on the same grounds. Each of the three latter species was described from one station only, with no illustrations provided, and in the case of *G. pavillardi*, with no size range provided.

The present author's choice of *G. polygramma* Stein as the name for the local species is based on the fact that although it resembles *G. turbynei* Murray and Whitting in its early stages of development, and also *G. pavillardi* Kofoid and *G. reticulata* Kofoid at other stages, it most resembles *G. polygramma* in its plate pattern, shape of significant plates, reticulation, antapical spine development, and ecdysis; allowing for variation within the group at a subspecific level. *G. polygramma* is the earliest described species within the group.

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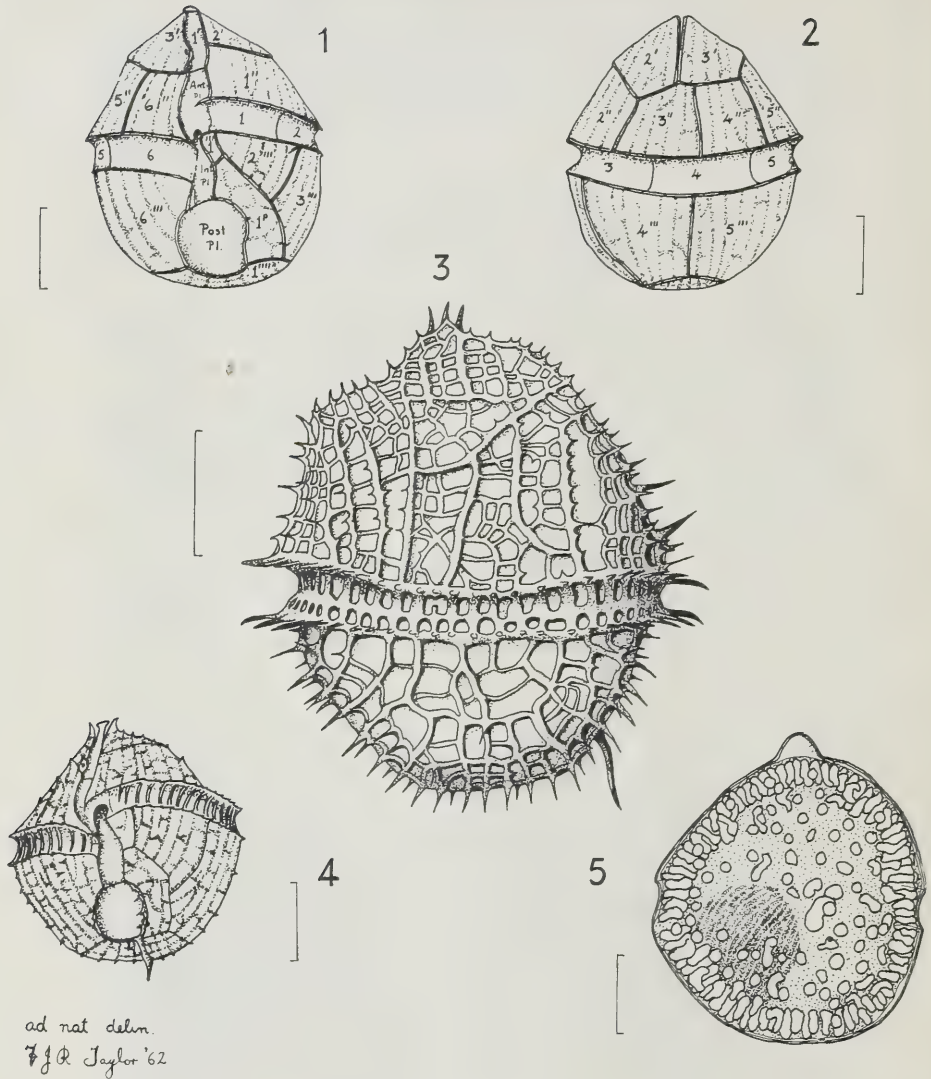


PLATE I
(Scale represents 10 μ)

- FIG. 1.—Ventral view of young theca, showing plates.
 FIG. 2.—Dorsal view of same.
 FIG. 3.—Older spiny theca, left side.
 FIG. 4.—Ventral view, intermediate stage.
 FIG. 5.—Cyst showing new theca developing.